Fish Fauna of the Western Caribbean Upper Slope

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THE importance of studies concerning offshore benthic marine habitats and associations of animals is gradually being realized. The concept of the marine environment is changing from one of extensive, homogeneous habitats with vague boundaries and randomly dispersed individuals, to one of diverse and well-defined habitats which closely control the composition and distribution of associated faunas. Basic descriptions of these distributions are required as bases for more advanced ecological investigations.

Previously a qualitative and quantitative description of the total upper Continental Slope fish fauna in a tropical region has not been available. It is the purpose of this paper to provide such a description for the western Caribbean Sea.

Although the general nature of the Continental Slope fauna has been known since the early days of modern deep-sea exploration (e.g., Agassiz, 1888), little new knowledge concerning the biology of this major environment has been contributed since the turn of the century. As part of a program to expand the commercial fisheries of the United States, the U. S. Bureau of Commercial Fisheries has conducted exploratory trawling surveys of the upper-slope environment in the Gulf of Mexico and off southeastern United States since 1950. Early findings were encouraging and additional work showed that commercial concentrations of the red shrimp, *Hymenopenaeus robustus*, occurred in the northern Gulf and off southwestern and eastern Florida (Springer and Bullis, 1954; Bullis, 1956; Bullis and Rathjen, 1959; Bullis and Cummins, 1963; Thompson, 1967; and Roe, 1969).

Subsequently, explorations were extended to the Caribbean and Cayman Seas, Bahamas, Greater and Lesser Antilles, and off northeastern South America. These continuing surveys have furnished data for an initial assessment of the upper-slope fauna for most of the tropical western Atlantic between Cape Hatteras, North Carolina and the easternmost tip of Brazil. Some areas of high productivity have been effected off the east coast of Florida in an area 1.6 to 3.2 km wide between 29° and 30° north latitude. In addition to the field records, representative samples of the fauna have been, and are presently, routinely collected and distributed to co-

operating systematists. Results of these surveys and laboratory identifications are incorporated into the automatic data retrieval system of the Bureau's Pascagoula, Mississippi Exploratory Fishing and Gear Research Base. Faunal lists and capture records from all phases of the exploratory fishing program are periodically published (Springer and Bullis, 1956; Bullis and Thompson, 1965). The history and activities of the program have been recently summarized by Bullis (1964).

Two exploratory fishing surveys of the upper slope in the western Caribbean were made by the R/V *Oregon* Cruise 46 in late summer of 1957 and Cruise 78 in late spring of 1962. On the first cruise, field data were incomplete and emphasis was on obtaining extensive qualitative collections of fishes and invertebrates. The identified collections from the first cruise enabled detailed records of species occurrence and abundance to be maintained during the second cruise. These are reported and discussed here.

STUDY AREA

The study area is shown in Fig. 1 along with the locations of the 44 stations evaluated in this report. Observations were made in the 75- to 500-fathom depth range in four general areas; off Rosalind Bank, northern and southern Nicaragua, and western Panama. This is a north-south distance of about 800 km and encompasses most of the western Caribbean.

The Continental Shelf within the northern portion of the area is roughly triangular, narrowing to less than 32 km at the western and southern extremities and broadening to some 200 km between Cabo Gracias a Dios and the northeastern corner.

The shelf proper is a limestone bank, for the most part, with depths from 10-30 fathoms. It is heavily covered with surface or near-surface reefs and many cays (keys) within the 20-fathom isobath. The bottom is irregular and covered with sponge and corals beyond the 20-fathom isobath, making sampling with a trawl, or even a dredge, difficult. Within the 10-fathom isobath are extensive stretches of smooth bottom, consisting mostly of sand and calcareous mud, and here considerable commercial shrimp trawling is conducted periodically.

The shelf edge, or break, varies from 30-40 fathoms below the surface. The bottom to depths of 75-100 fathoms is very rough and
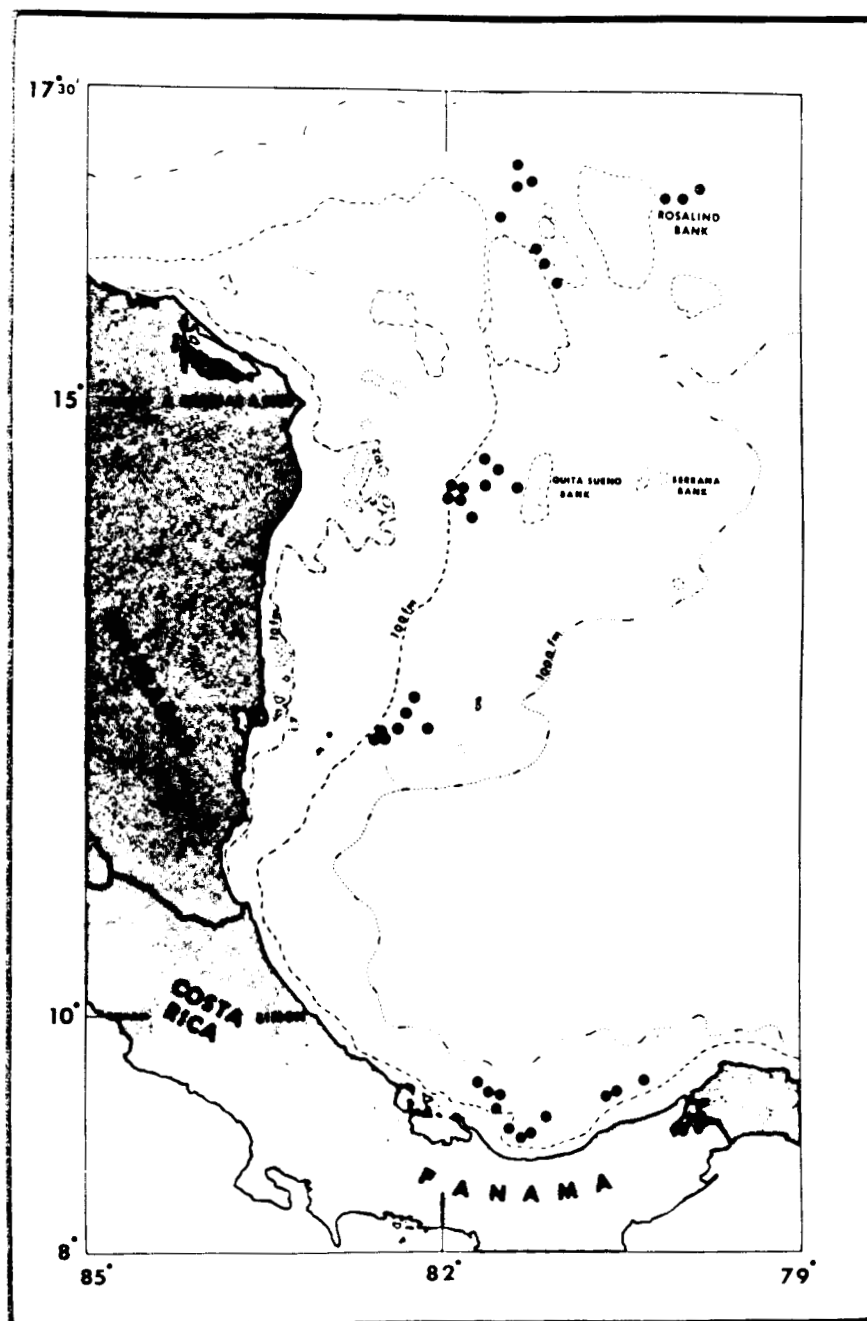
Fig. 1. Study area in the southwestern Caribbean Sea showing positions of trawl stations during R/V *Oregon* Cruise 78. Each dot represents one or more stations.

also generally untrawlable. Along the northern edge of the shelf, the upper Continental Slope has temperature gradients of 3-18C; the distance between the 75- and 500-fathom isobaths ranges from 3.2-2.2 km. A large bank about 56 km long and several small banks, all less than 20 fathoms deep, are connected to the northeastern corner of the shelf by depths of 100-150 fathoms. A 16- to 24-km wide channel with depths of 250 to 400 fathoms separates the large bank from Rosalind Bank to the northeast. Northwest of the channel between the Continental Shelf and Rosalind Bank there is a broad, flat area, seemingly a submarine alluvial fan, of about 100 square km at a fairly consistent depth of 150 fathoms.

South of Rosalind Bank the Continental Slope is broad all the way to about 12° north latitude. The horizontal distances between the 100- and 1,000-fathom isobaths range from 105-39 km, with an average of about 76 km. Within these limits are several large banks and small islands. Serranilla Bank (16°N, 80°W) and Quita Sueno Bank (14°30'N, 81°W) are separated from the shelf by depths less than 500 fathoms. The other major structures, Serrana and Roncador Banks and Old Providence and St. Andrews Islands, are separated from the shelf by depths of 800 fathoms or more. The distance of the 500-fathom isobath from the shelf edge is 63 km at the northern end (15°N), 21 km at 13°30' north latitude, 51 km at 13° north latitude, and about 13 km off Bluefields, Nicaragua at 12° north latitude. Between 15°N and 12°30' north latitude the slope gradient is very gentle, ranging from less than 1° to about 4°. The bottom there consists of gray and white mud. The sampling and sounding transects run by the R/V *Oregon* indicate that this area offers several thousand square km of good trawling bottom. South of 12°30' north latitude the slope is steep and rough, with numerous precipitous faces and gullies to depths of at least 500 fathoms. The bottom is calcareous.

The Continental Shelf in the Golfo de los Mosquitos is narrow, averaging 8-16 km wide, and has a topography and bottom invertebrate fauna similar to the shelf off eastern Nicaragua. The upper slope has a moderate smooth gradient, as off most of Nicaragua, and, in general, no trawling difficulties were encountered.

TEMPERATURES

The western boundary current is the dominant hydrographic feature in the West Indian region. This system is composed of ex-

tensions of the equatorial currents that enter the eastern Caribbean Sea over the Antilles Ridge. The strong, mixed Caribbean current passes through Cayman Sea and the Yucatan Channel, turns easterly and then flows through the Straits of Florida with increased velocity, emerging as the Florida Current. This current follows the southeastern coast of the United States to Cape Hatteras where it leaves the coast, and, with the union of the Antilles Current, it becomes the Gulf Stream. Along the edges of this system numerous eddies develop, especially in the southwestern Caribbean and Cayman Seas and between Jamaica and Cuba. There are also several large, apparently semi-permanent, eddies in the Gulf of Mexico (Sverdrup, Johnson, and Fleming, 1942).

This warm, northerly flowing current has a profound influence on the Continental Shelf fauna of the region and accounts for the northerly extension of established populations of tropical animals into the Gulf of Mexico and to Cape Hatteras at 35°20′ north latitude (Ekman, 1953, p. 46; Cerame-Vivas and Gray, 1966; Struhsaker, In Press). As Cerame-Vivas and Gray point out, these warm, western boundary currents result in the characteristic "trumpet shape" faunal distributions of the tropical regions of the world ocean.

In a different manner, the western boundary current greatly influences the West Indian upper-slope fauna. Because of the density relations within a stratified fluid in motion in the Northern Hemisphere (when looking at a cross-section of the current in the direction it is flowing) the lighter (warmer) water lies to the right of the current and the denser (colder) water lies to the left. This results in a strong horizontal temperature gradient maintained by a cross circulation that advects warm water on the right side of the current, while cold, deep water is brought near the surface on the left side of the current (Dietrich, 1963, p. 535). Thus, the upper slopes of the continental Western Hemisphere have temperatures of 8-12 C at depths of 220 fathoms, whereas temperatures of 14-17C are found at the same depth over the upper slopes of the Bahamas, Greater Antilles, and much of the Lesser Antilles (see Chart V of Sverdrup, Johnson, and Fleming, 1942). Struhsaker (In Press) has pointed out that this results in two natural divisions of the upper-slope environment in the tropical western North Atlantic, which may be termed the Continental Slopes and the Insular Slopes. Exploratory trawling surveys have shown striking differences between

the faunal composition of the two divisions at similar depths. That species common to both divisions occur much deeper over the Insular Slopes is also readily apparent. This effect seems to be exceptionally well demonstrated in the Straits of Florida where the two major divisions of slope faunas of the region occur on opposite sides of the Straits, only about 65 km apart. We hope this paper will provide some basis for the eventual detailed analyses and comparisons of the two faunal divisions.

Normally, bottom temperatures at the 100-fathom isobath of the Continental slopes (hereafter distinguished from the Insular slopes) range between 15-21 C, whereas at 200 fathoms temperatures are from 8-12 C. Eighteen bottom temperatures were obtained during the survey with an experimental minimum temperature recording device that was previously calibrated with a protected thermometer. The results are shown in Fig. 2 along with data on indicated bottom temperatures in the study area from Parr (1937). The resulting bottom temperature profile for the study area agrees well with the temperatures presented by Fuglister (1960) and Stewart (1962) for this region.

Because of the temperature gradients in the western boundary current as mentioned above, the deep permanent thermocline layer (PTL) of the western North Atlantic, is centered at about 200 fathoms here (Struhsaker, In Press). As Fig. 2 shows, the PTL (between about 19-7C) encompasses most of the upper Continental Slope zone in the study area. Although the upper-slope bottom temperatures are below the depth of seasonal influences, Struhsaker (In Press) presented evidence that internal waves in the PTL could effect short-period temperature changes of at least 3 C. He also hypothesized that these temperature changes might effect local changes in the depth distribution of some of the more mobile inhabitants of the upper slopes.

METHODS

The sampling gears used in this study were 12.2 m flat and semi-balloon shrimp trawls (Bullis, 1951). The netting was 5 cm stretched mesh (#18 thread cotton) in the trawl bodies and 4 cm stretched mesh (#42 thread cotton) in the codends. These trawls cover a path 6.7-7.3m wide under usual conditions when spread with 1.8 m trawl doors. Using a single float, the trawl has a vertical opening of about 1.5 m. The footrope rides very lightly on the
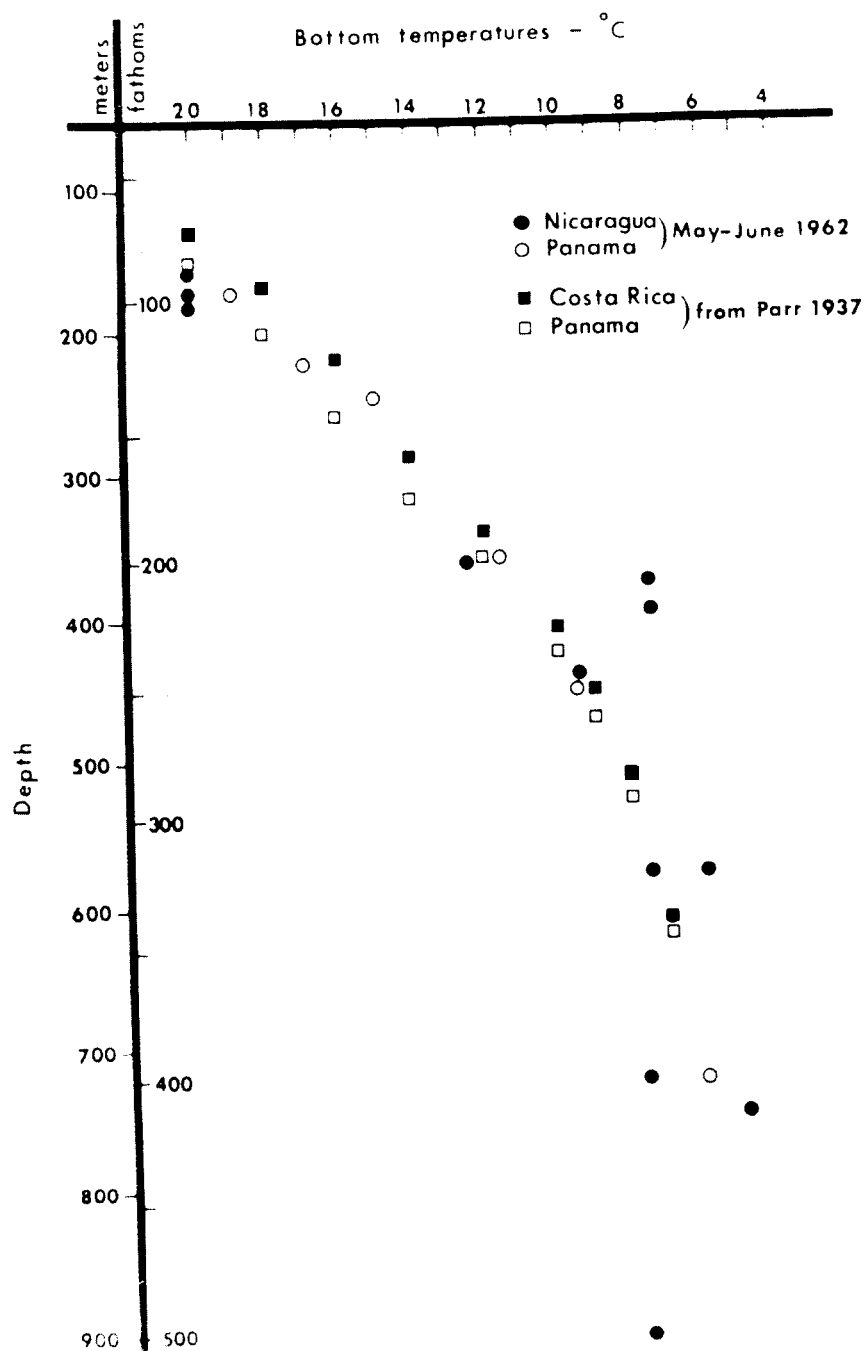
Fig. 2. Bottom temperature profile for Continental Slope depths in the southwestern Caribbean Sea.

bottom and a "tickler chain" attached to the bottom rear corner of each door rides about .6-.9 m in front of the footrope and incites the more active benthos to swim or jump off the bottom into the path of the trawl.

Because of the number of variables involved, quantitative data on animal populations sampled with shrimp trawls can be developed only in very general terms. Sampling periods of 1, 2, 3, and 4 hours were attempted, but frequently they were interrupted because trawling hazards appeared on the depth sounder-recorders. Navigation was by celestial means and loran fixes except in a few cases of radar positioning. We attempted to maintain a constant speed of 2 to 3 knots (1.0-1.4 m/second) but current conditions may have varied the range of speeds as much as ±2 knots (1 m/second) in some areas. Quantifying these data is further complicated because shrimp trawls capture only a portion of the animals in their paths. For example, recent motion picture analyses (unpublished) of shrimp trawl performance by the Bureau of Commercial Fisheries Gear Research Unit, Pascagoula, Mississippi, show that escapement of royal-red shrimp (*Hymenopenaeus robustus*) might be as high as 90 per cent of all shrimp encountered by the trawl.

Despite these difficulties, some attempt must be made to quantify and interpret these observations on the upper-slope fauna to provide bases for more detailed and sophisticated investigations. Until more efficient sampling gears are devised, we feel that analysis of a large number of shrimp trawl samples will provide some of these bases. Because of the known inefficiency of the trawls, all biomass and numerical density figures given in this paper should be considered minimal. To determine the area sampled in each depth range, we assumed an average on-bottom trawl speed of 2.5 knots (1.2 m/second) and average net opening of 7 m, which resulted in a sampling rate of 3.2 hectares per hour.

The amount and distribution of sampling effort and the numbers and weights of fishes taken are shown in Table 1. Fifty-fathom depth intervals were selected as the most practical because of sampling distribution. The number of stations in each 50-fathom depth range varied from 1-9, whereas the number of hectares sampled varied from 9.6-60.8. The 44 trawling stations represent a total of 79.6 hours of on-bottom sampling time during which about 29,700 fishes were captured. At each station the fishes and the crustaceans were sorted from the catch and counted. Lengths and

TABLE 1

Distribution of Sampling Effort, Number of Families, Number of Fish taken, Pounds of Fish taken, Density and Biomass by Depth in the Study Area

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Total no. stations	6	9	8	9	3	4	2	1	2
Total no. hectares sampled	19.2	34.9	60.8	49.6	20.8	30.7	13.1	9.6	16.0
Total no. of families taken	31	36	37	41	33	34	18	8	8
Total no. of fish taken	1827	3967	9796	9451	1838	2176	422	25	174
Average no. of fish/ hectare sampled	95.2	113.7	161.1	190.5	88.4	70.9	32.2	2.6	10.9
Total no. of kgs. of fish taken	150	218	350	418	104	150	45	9	27
Average no. of kgs./hectare	7.8	6.2	5.8	8.4	5.0	4.8	3.4	1.0	1.7

weights were recorded for most species of the readily identifiable fishes. Measurements were made using measuring boards with 0.5 cm units. Extensive zoological collections were made during the survey, most of which are in the collections of the U. S. National Museum and the Bureau's Tropical Atlantic Biological Laboratory, Miami, Florida.

RESULTS AND DISCUSSION

Composition, Abundance, and Distribution. Any attempt to report on a large portion of the slope fauna of the western Atlantic south of 35° north latitude is complicated by the limited taxonomic knowledge of many important groups of animals and lack of identification keys suitable for field use. An extreme example of the unknown nature of the fish fauna in the study area is represented by the Scyliorhinidae (See Appendix I). This family was represented by four forms; *Galeus arae*, a new species of *Galeus*, a new species of *Scyliorhinus*, and an undescribed genus and species. Springer (1965) has since described these forms (See Appendix I). Of three species of chimaeras present, only one, *Hydrolagus alberti*, has been recorded as a member of the western Atlantic fauna. A second species of *Hydrolagus* probably represents what has been considered an endemic of the northwestern Atlantic, and the third an undescribed species of *Neoharriotta* (Bullis and Carpenter, 1966), previously considered a monotypic genus in the eastern Atlantic. Other groups that presented identification problems were the families Congridae, Brotulidae, Gadidae, and Ophidiidae, and the peristediid genus *Peristedion*.

The benthic fishes taken during the survey represent 60 families and an estimated 140 species; however, in the field only about 73 were identified to species, 21 to genera and the remainder to family. All of the batoid fishes were preserved and later identified by William C. Schroeder, Woods Hole Oceanographic Institute. These field and laboratory identifications resulted in a total of 127 species and species groups of demersal fishes, which are listed in Appendix I.

We should state here that we consider all fishes listed to primarily occupy the demersal habitat as adults. Thompson (1963) considers the bathyalbenthic bottom community to be a richly populated ecotonal belt, which grades into the pelagic layers above

and the benthic layers below. The belt is inhabited not only by endemic species, but also occasionally by truly benthic or pelagic animals. Fish inhabitants of this belt are easy to capture in our bottom trawls; therefore, we consider demersal fish species to be not only those that rest upon or burrow in the bottom but also those that are free-swimming but still closely associated with the bottom.

In general composition, some 75 per cent of the identifiable species taken in the study area are widely distributed at similar depths along the Continental Slopes of the tropical western Atlantic region. About 18 per cent of the species appear to be approaching the southern limit of their geographic range; 3 per cent are nearing the northward limit; and the remaining 4 per cent are known only from the southwestern Caribbean. Therefore, 93 per cent of the western Caribbean species are found in the Gulf of Mexico and along the southeastern coast of the United States, whereas only 78 per cent are known from the southeastern Caribbean and off northeastern South America (as derived from available literature sources and extensive unpublished distribution data at the Exploratory Fishing and Gear Research Base, Pascagoula, Mississippi).

The depth distribution and numerical abundance of each family and species group is given in Appendix I. The relative abundance of each family and the bottom temperatures in each 50-fathom depth zone are shown in Figs. 3a and 3b. Families that were present, but comprised less than 1 per cent of all the fishes taken, are shown as a straight line, whereas the dashed line indicates that the family was not represented in that depth range.

Fifteen families were numerically dominant in the study area. Seven of these achieved dominance by the abundance of single species: Caproidae—*Antigonia combatia*; Polymixiidae—*Polymixia lowei*; Triglidae—*Bellator egretta*; Zeidae—*Zenion hololepis*; Grammicolepidae—*Xenolepidichthys dahlgleshi*; Neoscopelidae-*Neoscopelus macrolepidotus*; and Chaunacidae—*Chaunax pictus*. The remaining eight families achieved their dominant status by the occurrence of from 2-14 species.

Upon leaving the shelf, 26 per cent of the families represented in 75-100 fathoms are lost. At 150 fathoms 39 per cent have been lost; 49 per cent at 200 fathoms; 59 per cent at 250 fathoms; and at 350 fathoms 88 per cent have disappeared. Of the remaining four families, one drops out at 400 fathoms, one at 450, and two persist to the limits of the study depths. However, of 31 families found

on the outer shelf (75-100 fathoms), six (Apogonidae, Scorpaenidae, Ogcocephalidae, Brotulidae, Ophidiidae, and Congridae) are composed of diverse species that represent their respective families over a wide bathymetric range, and six additional families (Caproi-

Fig. 3a. Relative abundance of families on the Upper Continental Slope of the southwestern Caribbean Sea as percentage of total fishes sampled from each depth range.

dae, Triacanthodidae, Percophididae, Polymixiidae, Trachichthyidae, and Gempylidae) are shallow-water extensions of families that may be considered as typical inhabitants of the upper Continental Slope.
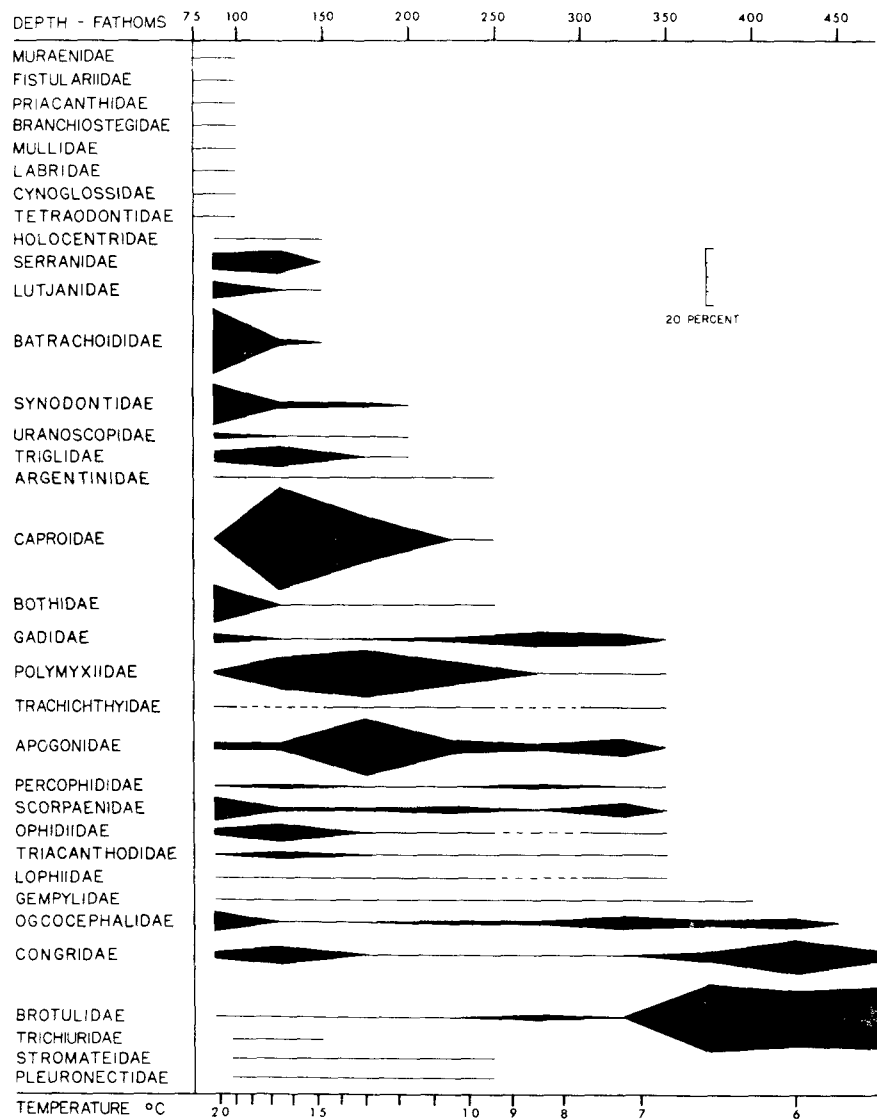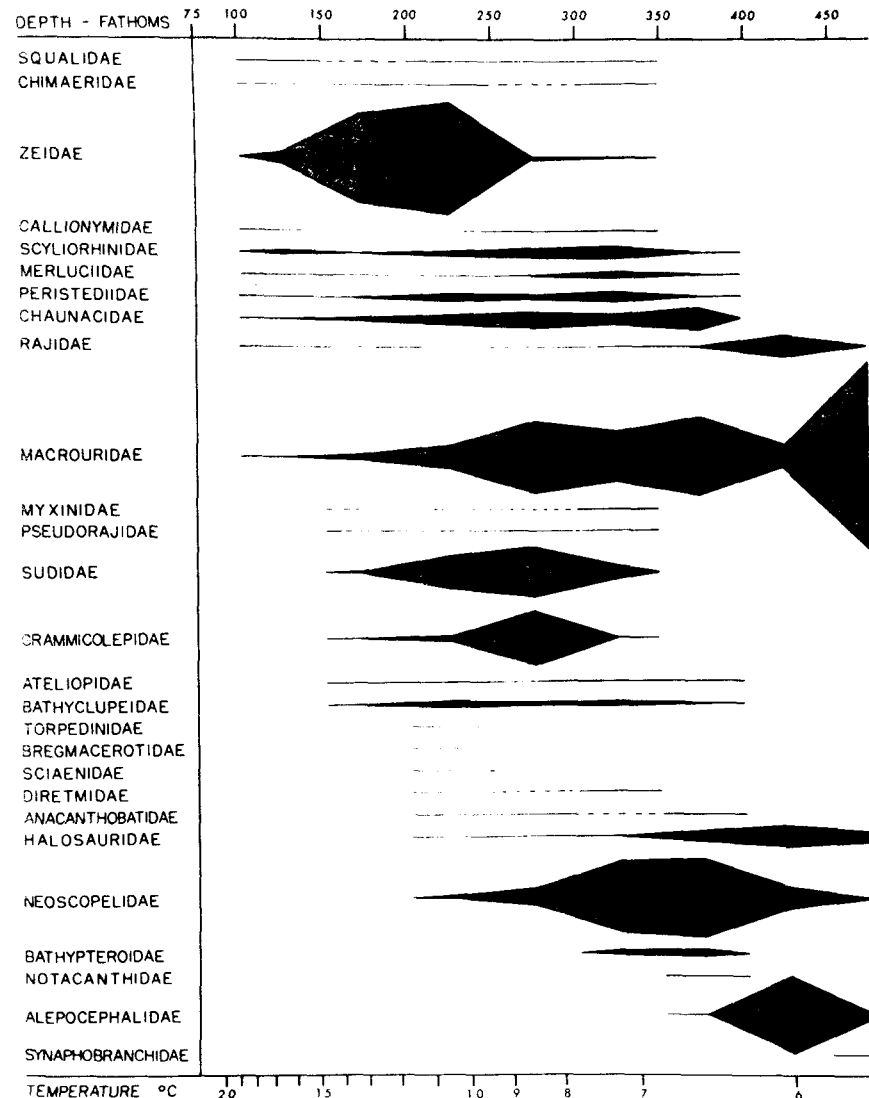

Fig. 3b. Relative abundance of families on the Upper Continental Slope of the southwestern Caribbean Sea as percentage of total fishes sampled from each depth range.

Within the 101- to 150-fathom range, we first find many families that might be considered as typical inhabitants of the upper Continental Slope in the Caribbean region. Nineteen families (Caproidae, Triacanthodidae, Percophididae, Polymixiidae, Anacanthobatidae, Pseudorajidae, Merluciidae, Callionymidae, Scyliorhinidae, Peristediidae, Zeidae, Chaunacidae, Sudidae, Chlorophthalmidae, Myxinidae, Bathyclupeidae, Ateleopidae, Chimaeridae, and Neoscopelidae) were taken in the study area. The four numerically dominant families in numbers of individual fish are the Caproidae, Polymixiidae, Serranidae, and Triglidae, respectively. The last two families are typical shelf inhabitants, with some members (i.e., *Serranus phoebe, Bellator* sp.) extending slightly beyond the edge of the Continental Shelf.

In the 151- to 200-fathom range the numerically dominant families are all typically upper-slope groups. Four families make up 83 per cent of the total number of fish taken in these depths: Zeidae (32 per cent), Apogonidae (18 per cent), Caproidae (17 per cent), and Polymixiidae (16 per cent). The typical shelf families decrease in number rapidly.

The zeids are still the dominant family in the 201- to 250-fathom range and comprise 39 per cent of the total number of fishes taken in these depths. In abundance, they are followed by the Sudidae, Macrouridae, and Polymixiidae. This marks the first appearance of sudids and macrourids in any numbers. The Caproidae is poorly represented in this depth range, decreasing rapidly in abundance after being the dominant family in 101-150 fathoms.

The Macrouridae comprise 26 per cent of the fish sampled in the 251- to 300-fathom depth range and assume dominance. Large numbers of grammicolepids are present only in this depth range. The Sudidae remain numerically important and are followed by the first appearance of the Neoscopelidae.

The Neoscopelidae assume dominance (27 per cent) in the 301- to 350-fathom depth range and are followed by the macrourids (18 per cent). Most of the remaining fish caught are more or less uniformly distributed among eight families, six of which were typically upper-slope forms. Beyond 300 fathoms the upper-slope families are numerically less important.

The Neoscopelidae and Macrouridae are still the dominant families (28 per cent) each in the 351- to 400-fathom depth range,

closely followed by the Brotulidae (24 per cent), which makes its first appearance as a numerically important family. The upper-slope families are virtually unrepresented in this depth range where, along with the brotulids, there is the introduction of the Halosauridae, Congridae, and Bathypteroidae as numerically important groups.

In 401-450 fathoms the alepocephalids and brotulids are dominant and, collectively, account for 48 per cent of the fish taken in this depth. Further net "loss" of families in this depth range reduces the total number of families to eight; however, only one station was occupied in that depth range.

Eight families are present in the 451- to 500-fathom depth range, of which the macrourids are overwhelmingly dominant (68 per cent). The remaining seven families are either typically abyssal or are those with wide bathymetric distributions.

Distribution Pattern. The general pattern that emerges from these abundance and distribution data is typical of most animal aggregations. Although many groups are present in an area, the total faunal composition is dominated by only a few taxa. In passing from one depth zone to another, these dominant taxa arise, gain dominance in a particular zone, and then gradually lose importance and disappear. Although records were not kept on the weights of the species and species groups taken at each station, examination of the numerical density data in conjunction with known weight ranges for each group indicates that when a family is among the numerically dominant in a particular depth range, it is usually one of the dominant groups with regard to biomass.

Although there is, in general, a gradual replacement of one dominant group by another from zone to zone, the data of Fig. 3 seem to show two major trends. The first is the disappearance and appearance of many families between 75 and 100 fathoms. The second is the apparent major loss of families in depths greater than 350 fathoms. This effect is further illustrated in Fig. 4 where the total number of families taken in each depth range is given along with the number of families "gained" and "lost" in each depth range when progressing from lesser to greater depths. The net change for each depth range is shown at the top of its column. The total number of families gradually *increases* from the shelf edge to a high in the 201- to 250-fathom depth range. The number gradu-
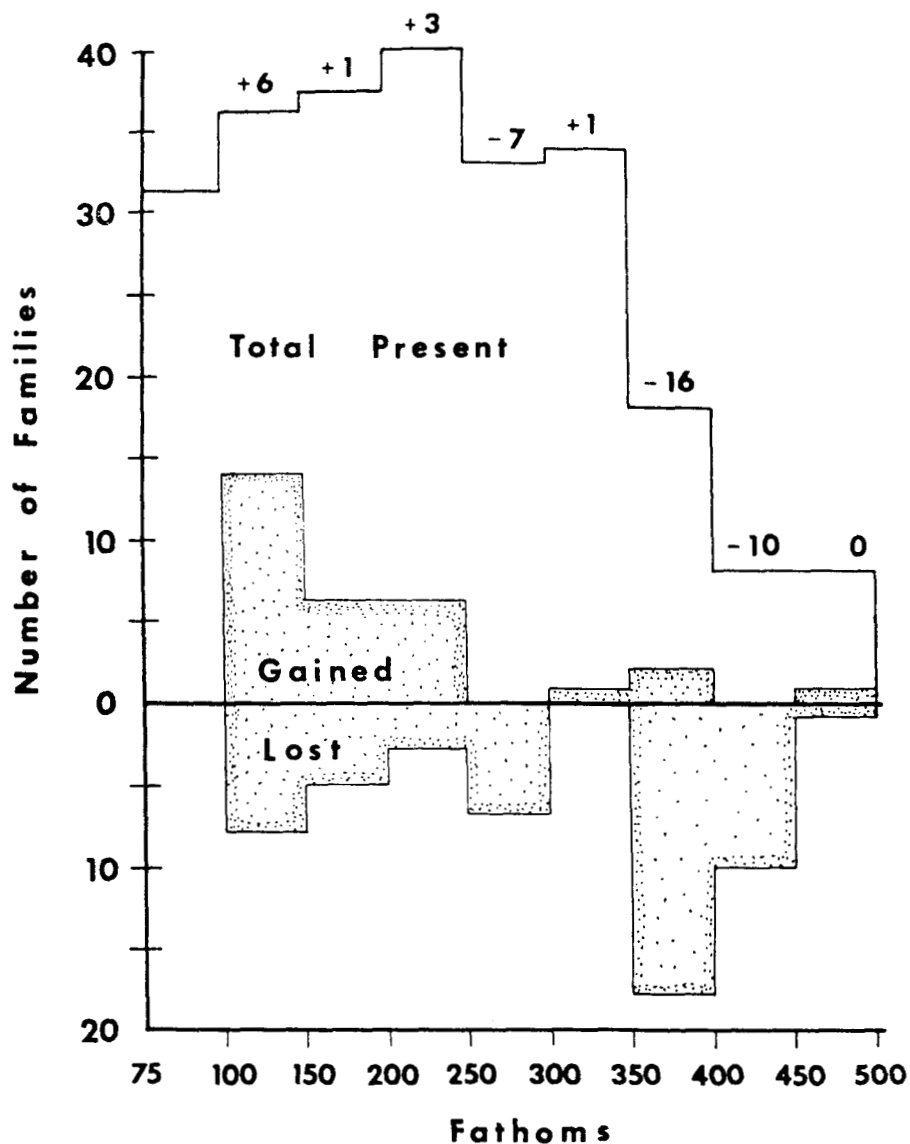
Fig. 4. Total number of families present in each depth range and the number of families "gained" and "lost" in each depth range when progressing from lesser to greater depths. Net change for each 50-fathom interval shown at top of histogram.

ally diminishes in the next two depth ranges, but is suddenly reduced between 351-400 fathoms and 401-450 fathoms.

This pattern is interpreted as follows: upon leaving the shelf, the familial composition of the ichthyofauna undergoes a major

TABLE 2

Estimated Minimum Standing Crop for the Indicated Depth Ranges
within the Study Area

Depth range in fathoms	Kilograms/hectare			
	Fish	Crustaceans	Other Invertebrates	Total
75-100	7.8	0.9	3.1	10.9
101-150	6.2	0.3	4.5	11.0
151-200	5.8	1.2	2.0	9.0
201-250	8.4	2.7	1.7	12.8
251-300	5.0	0.9	1.3	7.2
301-350	4.9	1.3	1.5	77.7
351-400	3.5	2.4	0.4	6.3
401-450	1.0	0.0	0.4	1.4
451-500	1.7	0.4	0.7	2.8

change, resulting in an overall gain in families from the outer shelf zone (75 to 100 fathoms). Conditions stabilize in the next few depth ranges: with the small exchange of families that occurs, there is a general increase in the total number of families present to 201-250 fathoms. In the next two depth ranges, however, only one new family is introduced, whereas eight are lost. The great reduction of family numbers between 351 and 450 fathoms is due to the loss of 26 families with only two additions.

The estimated minimal standing crop of fishes within the study area is given in Table 2. The total biomass generally decreases upon leaving the Shelf edge but increases to a peak in the 201- to 250-fathom depth range. Beyond these depths the biomass decreases with depth. Whereas the estimated biomass of fishes follows this pattern, the echinoderms, sponges, and mollusks exhibit a generally decreasing biomass with increased depth. The crustaceans exhibit an increased "standing crop" in the 201- to 250-fathom and 351- to 400-fathom depth ranges. This is probably due partially to quantities of *Hymenopenaeus robustus* and *Nephrops binghami* in the 201- to 250-fathom range and *Plesiopenaeus edwardsianus* in the deeper depth range.

Upper-Slope Association. On the basis of the above data, there appears to be an association of fishes that is characteristic of the upper Continental Slope. The upper limit of this fauna in the 75-
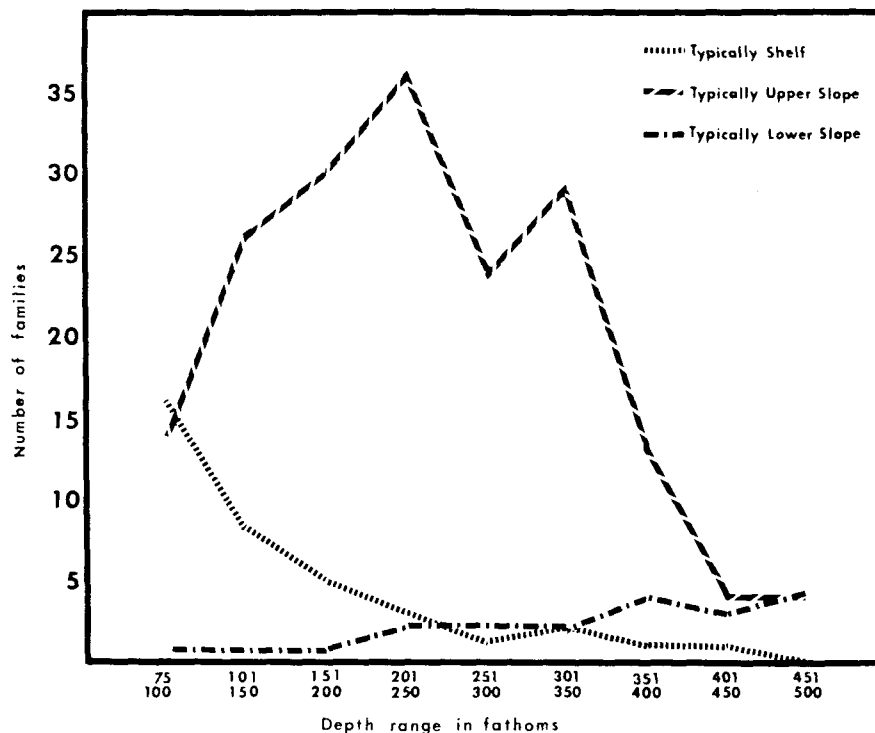
Fig. 5. Numbers of families at descending depth levels considered representative of shelf, upper-slope, and lower-slope ichthyofauna.

to 150-fathom depth range is an exchange area where typically shelf families are replaced by upper-slope families. The lower limit of upper-slope fauna is demarcated by the drastic reduction of total number of families present and replacement of upper-slope families with lower-slope families at depths greater than 350 fathoms. The shelf families are defined here as those that have greatest numerical density in depths between 75-100 fathoms. Upper-slope families are considered to be those that have the greatest density between 101-350 fathoms, and lower-slope families those greatest between 351-500 fathoms. The number of families in each category present in each depth range is shown in Fig. 5. As expected, the number of shelf families greatly diminishes beyond 100 fathoms and none are present in the 451- to 500-fathom depth

range. The lower slope families exhibit a similar trend from greater to lesser depths, reaching a peak number between 201-250 fathoms.

Although we have observed this enriched, distinctive upper-slope fauna in other areas of the tropical western North Atlantic, the data presented here represent the first quantitative analysis of this faunal association. In the western Caribbean, this association is distributed roughly between the 19 C isotherm (100 fathoms) and the 7 C isotherm (350 fathoms). These temperatures delimit the deep, permanent thermocline layer of the western North Atlantic region where it contacts the Continental Slope. There the fauna flourishes at depths of the 10 C isotherm (225 fathoms), diminishing quantitatively and qualitatively above and below this depth over the slope.

Schroeder (1955) reported the results of extensive trawling explorations of the Continental Slope in the western North Atlantic between Delaware Bay and Nova Scotia. About 75 species of bottom fishes were taken at 259 trawling stations in depths of about 50-730 fathoms over a two-year period. Of those species listed for the New England slope, the following eight were also taken in the western Caribbean: *Myxine glutinosa, Argentina striata, Parasudis truculentus, Merluccius albidus, Coelorhynchus carminatus, Zenopsis ocellatus*, and *Urophycis regius* (the last species was taken in the western Caribbean, but is not listed in Appendix I because detailed counts were not maintained for it). Schroeder (1955, p. 366) also presented estimates of the standing crop of slope fishes off New England. A comparison of Schroeder's figures (converted to kg/ha) for that region and our values (Table 2) are as follows: 101-200 fathoms, 17.9 vs. 6.0; 201-300 fathoms, 48.1 vs. 6.7; 301-400 fathoms, 50.4 vs. 4.1; 401-500 fathoms, 36.9 vs. 1.3. These data would indicate that the standing crop of fishes on the slope region of the northwestern Atlantic to be about 3, 7, 13, and 28 times as great as in the Caribbean. These data, however, should be compared only in a very general manner because Schroeder's estimates are based on catches of 18.2 m trawls with 7.6 cm mesh webbing, whereas our estimates are based on catches of 12.2 m trawls with 5 cm mesh webbing. As Schroeder (1955, p. 364) points out, bottom trawl catches seem to increase exponentially with increased trawl size. It thus appears that the New England slope ichthyofauna is richer quantitatively, but poorer qualitatively than that of the western Caribbean, as would be expected.

TABLE 3

Mean Lengths (mm) of Fishes Measured by Depth

Depth range (fathoms) Species	75 100	101 150	151 200	201 250	251 300	301 350	351 400	(n)
Antigonia combatia (TL)	97	121	—	—	—	—	—	(944)
Bathypterois bigelowi (FL)	—	—	—	—	134	118	123	(58)
Bembrops gobioides (TL)	—	—	195	180	193	—	—	(69)
Chaunax pictus (TL)	—	62	102	118	122	130	190	(1275)
Chlorophthalmus agassizi (TL)	—	—	72	136	148	145	—	(574)
Parasudis truculentus (TL)	—	—	161	205	220	—	—	(104)
Coelorhynchus carminatus (SD)	—	—	54	59	65	59	—	(273)
Cyttopsis roseus (TL)	—	—	—	93	110	—	—	(74)
Galeus arae (TL)	—	—	259	277	251	275	—	(344)
Merluccius albidus (TL)	—	—	275	290	365	415	—	(130)
Neoscopelus macrolepidotus (SL)	—	—	—	—	91	94	126	(762)
Nezumia bairdii (SD)	—	—	48	47	56	52	72	(408)
N. hildebrandi (SD)	—	—	—	32	36	—	44	(253)
Parahollardia schmidti (TL)	—	—	112	138	—	—	—	(90)
Polymixia lowei (TL)	97	129	136	153	127	—	—	(1489)
Setarches parmatus (TL)	—	—	86	103	—	127	—	(368)
Synagrops bella (FL)	—	98	125	158	182	167	—	(717)
Xenolepidichthys dalgleishi (TL)	—	—	95	102	88	—	—	(324)
Zenion hololepis (TL)	—	59	63	78	71	—	—	(635)

TL, total length; SL, standard length; FL, fork length; SD, tip of snout to origin of first dorsal.

Size and Depth. Extensive size-frequency data were taken for 19 species of fishes. They are summarized in Table 3 as mean sizes for each 50-fathom depth range. Species that were selected are readily identifiable and are a major component of the tropical western Atlantic upper-slope ichthyofauna. With a few notable exceptions, such as the peristidiids, ophidiids, brotulids, gadids, and congrids (most present identification problems now) these species represent a rather typical cross-section of the upper-slope ichthyofauna.

Fifteen species (*Chlorophthalmus agassizi, Parasudis truculentus, Neoscopelus macrolepidotus, Nezumia hildebrandi, N. bairdii, Coelorhynchus carminatus, Merluccius albidus, Cyttopsis roseus, Zenion hololepis, Antigonia combatia, Parahollardia schmidti, Polymixia lowei, Setarches guentheri, Synagrops bella,* and *Chaunax pictus*) demonstrate an increased mean size with increased depth. All but *Chaunax* and *Polymixia* have a significant (at the 1 per cent level) linear correlation. A curvilinear relation for these two species is strongly indicated.

The mean lengths of the four remaining species (*Bathypterois bigelowi, Xenolepidichthys dahlgleishi, Bembrops gobioides,* and *Galeus arae*) are nearly constant at all depths. A positive correlation between size and depth was found in *Galeus arae.* However, a complex distributional pattern in this species related to sexual maturity and depth grouping may bias the data toward this relation (Bullis, 1967).

For the most part, each species reaches its greatest density somewhere toward the center of its depth range. Also, species showing a strong size-depth relationship tend to have greater bathymetric ranges than species that do not demonstrate such a relationship.

The direct relation between size and depth has been discussed in detail for *Pleuronectes* in the North Sea, where such differential distribution also varies inversely between size (age) and density (Graham, 1956). Size increase with depth has been shown for several western Atlantic Shelf species by Caldwell (1955, 1957, 1961).

Explanatory Theories. In seeking an explanation for the above data, the modes of reproduction of the species involved were considered. Teleostean species in which the young develop pelagically characteristically spawn large numbers of eggs, whereas species in which the young develop in demersal habitats produce only

moderate to small numbers of eggs (Mead, Bertelsen, and Cohen, 1964). On the basis of these general types of development, the two following hypotheses are given to account for the size-depth relations reported above.

First, species that increase in mean size with increasing depth and decreasing temperatures, and have a broad bathymetric range, produce pelagic eggs and/or larvae. The young of these species are carried various distances along the coasts and may be swept inshore over the Continental Shelves or offshore into oceanic areas. After developing to the pre-juvenile stage, they either descend gradually to some depth or undergo relatively small daily vertical migrations. The depths to which these individuals descend are limited by the temperature tolerances of that species at that particular stage in its life history. Our hypothesis requires that these pelagic young do not descend deeper than the Continental Shelves or the upper end of the species' demersal depth range on the upper slope. Individual pre-juveniles undergoing vertical movements over the shelf and upper slope eventually contact the bottom, but those carried to oceanic areas only descend to certain depths (depending upon the local temperature structure), never contact the bottom and are permanently lost to the primary population. The young of these species that find the bottom relatively quickly move to the habitat of their size and age group, which tends to be at lesser depths than the adults, because they are undergoing a temperature acclimation from the warm, epipelagic environment to the colder, demersal upper-slope environment. During development and maturation in this demersal habitat, young individuals gradually descend to depths occupied by the reproducing segment of the population. A few individuals wander into even greater depths, where decreased temperatures may slow their growth rate but increase their longevity. These latter individuals are the largest, but least numerous members of the population.

The second hypothesis is that species that change only slightly in mean size with depth, and usually occupy a more restricted bathic range, have demersal eggs and larvae or bear their young alive. The young of these species already inhabit the depths and temperatures occupied by the adult segment of the population. Thus, they do not undergo change from a warm, epipelagic existence to a cold, benthonic existence, and become more restricted in

demersal depth ranges while dispersing over the entire bathic range of the population.

Of the 15 species demonstrating a size-depth relation and for which we hypothesize pelagic young, nine are represented by pelagic larvae identifiable to the familial or generic level: Neoscopelidae (implied); *Chlorophthalmus*; and *Chaunax* (Mead, et. al., 1964); Macrouridae (Marshall, 1965); *Antigonia* (Berry, 1959); and *Merluccius* (Bigelow and Schroeder, 1953). Four of the remaining six species (*Synagrops bella, Setarches guentheri, Cyttopsis roseus, Zenion hololepis*) are represented at the familial level by larval specimens taken in epipelagic plankton tows during investigations off southeastern United States by the R/V *Theodore N. Gill.* The families of the two remaining species (*Polymixia lowei* and *Parahollardia schmidti*) have not been recognized in the *Gill* collections, but pelagic berycomorph and plectognath larvae are common (Jack Gehringer and Frederick H. Berry, Bureau of Commercial Fisheries, Biological Laboratory, Brunswick, Georgia, personal communication).

Two of the four species with no size-depth correlation and for which we hypothesize demersal eggs or larvae, are thought to have benthonic young. We assume the scyliorhynid *Galeus arae* to be viviparous (Stewart Springer, personal communication). The deep-sea iniomid fishes, which would include *Bathypterois bigelowi* under consideration here, produce a relatively small number of eggs that develop on or near the bottom (Mead, et al., 1964). The two remaining species, *Xenolepidichthys dahlgleishi* and *Bembrops gobioides*, may be considered as negative evidence supporting the above hypotheses since grammicolepid and percophidid eggs and larvae have not been recognized in the *Gill* epipelagic plankton collections (J. Gehringer and F. Berry, personal communication).

In the slope environment, size-depth relations appear influenced by two factors: vertical movements of population segments of species having planktonic eggs and larvae; and the physiological response of all populations to the direct relations of depth and temperature in slower growth, increased age, and greater maximum size with increased depth.

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APPENDIX I

Depth Distribution of Fish Families and Species in Average Density of Individuals per Hectare

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Myxinidae									
Myxine glutinosa			.02	.02		.10			
Scyliorhinidae		1.31				.10			
Galeus arae			1.21	2.78	3.37	3.13	.08		
Galeus cadenati			1.05	2.57	2.84	3.03	.08		
Scyliorhinus hesperius		.11	.05	.13	.53	.10			
Schroederichthys maculatus		1.20	.11	.08					
Squalidae		.17		.34	.05	.55			
Etmopterus bullisi						.36			
E. schultzi				.06	.05	.03			
E. virens				.22		.07			
Centrophorus granulosus				.02					
C. uyato						.03			
Squalus cubensis		.17		.02		.03			
S. blainvilli				.02		.03			
Torpedinidae				.02					
Torpedo nobiliana				.02					.06
Rajidae		.17	.41	.74	.20	.64	.31	.21	
Raja lentigenosa		.17							
R. teevani						.03			
Breviraja colesi						.06			
B. spinosa			.21	.16	.10				
Cruriraja poeyi				.22					
C. rugosa				.18	.10	.52		.21	

APPENDIX I (Cont.)

Depth range (fathoms)	75 / 100	101 / 150	151 / 200	201 / 250	251 / 300	301 / 350	351 / 400	401 / 450	451 / 500
Gen., sp. indeter.						.03	.31		.06
Pseudorajidae			.20	.18		.23			
Pseudoraja atlantica			.15	1.33	.24	.20			
P. fscheri			.15	1.33	.24	.03			
Anacanthobatidae				.46	.19		.31		
Anacanthobatis americanus				.46	.19		.31		
Chimaeridae		.06		.08					
Hydrolagus alberti		.06	.02	.04		.20			
Neoharriotta carri			.02	.04		.20			
Argentinidae	.16	1.15	.99	.85					
Argentina striata		1.15	.51	.85					
Gen., sp. indeter.	.16		.48						
Alepocephalidae							.31	.73	
Muraenidae	.05								
Gymnothorax ocellatus	.05								
Congridae	2.14	6.08	.31	.36	.29	.49	1.22	.31	.44
Synaphobranchidae									.13
Synaphobranchus kaupi									.13
Halosauridae				.32	.38	.39	1.37	.20	.38
Notacanthidae							.08		
Notacanthus analis							.08		
Synodidae	13.91	1.66	1.97						
Sudidae			1.57	23.03	15.05	3.42			
Chlorophthalmus agassizi			.71	20.26	14.42	3.42			
Parasudis truculentus			.86	2.77	.63				

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bathypteroidae									
Bathypterois bigelowi					.48	1.76	.99		
B. viridensis					.48	1.50	.38		
Bathypterois sp.						.26	.61		
Neoscopelidae				2.34	6.06	19.14	9.40	.21	.06
Neoscopelus macrolepidotus				2.34	6.06	19.14	9.40	.21	.06
Ateleopidae			.07	.02	.10	.03	.08		
Ijimaia antillarum			.07	.02	.10	.03	.08		
Gadidae	3.23	.14	.02	2.12	4.17	2.51			
Macrouridae		.20	3.94	18.26	21.93	12.78	9.39	.31	7.39
Steindachneria argenteus		.20	.49	2.20	.24	.10			
Coelorhynchus caribbaeus			1.09	.79					
C. carminatus			.90	2.59	4.09	.52			
Nezumia bairdii			1.46	6.30	4.38	8.70	.23	.10	.38
N. hildebrandi				2.22	8.70	1.89	.76		.63
Trachonurus sulcatus						.13	.38	.10	.31
Oxygadus occa							.23		.06
Gadomus longifilis					.14	.36	.38		.75
G. arcuatus							.31	.10	
Bathygadus vaillanti					3.03	.13	.92		1.31
B. favosus									2.63
B. macrops									.44
Hymenocephalus sp.				4.12	1.35	.95	6.18		.88
Cariburus sp.				.04					
Bregmaceriidae				.04					

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bregmaceros atlanticus				.04					
Merluciidae		.09	.05	1.58	.24	1.53	.08		
Merluccius albidus		.09	.05	1.58	.24	1.53	.08		
Fistulariidae	.05								
Fistularia tabacaria	.05								
Polymixiidae	1.09	12.74	26.23	15.47	.14	.03			
Polymixia lowei	1.09	12.74	26.23	15.47	.14	.03			
Trachichthyidae	.05		.02	.59		.03			
Hoplostethus sp.	.05		.02	.59		.03			
Holocentridae	.26	.03							
Myripristis jacobus	.26	.03							
Diretmidae				.02		.26			
Diretmus argenteus				.02		.26			
Zeidae		3.24	51.74	73.94	1.40	.78			
Zenion hololepis		2.90	50.95	72.40	.87	.62			
Cyttopsis roseus		.20	.54	1.52	.53	.16			
Parazen pacificus		.14	.25						
Zenopsis ocellatus				.02					
Grammicolepidae		1.15	2.85	17.32	.10				
Xenolepidichthys dahlgleishi		1.15	2.85	17.32	.10				
Caproidae	.36	41.73	26.83	.06					
Antigonia capros	.10	.23							
A. combatia	.26	41.50	26.83	.06					
Bathyclupeidae			.02	3.41	1.44	1.11	.08		
Bathyclupea argenteus			.02	3.41	1.44	1.11	.08		

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Serranidae	5.64	9.01							
Serranus phoebe	.89	.03							
Unidentified	4.75	8.98							
Lutjanidae	7.09	.95							
Lutjanus vivanus	1.30	.03							
Pristipomoides aquilonaris	.68								
Unidentified	5.11								
Priacanthidae	.26								
Pseudopriacanthus altus	.21								
Priacanthus arenatus	.05								
Apogonidae	2.50	4.58	28.48	10.08	3.85	4.24			
Synagrops bella	.36	4.38	9.26	7.02	1.97	.75			
Synagrops sp. 1			19.06	.61					
Synagrops sp. 2		.20	.16						
Epigonus pandionus				.65		.49			
Unidentified sp. 1	2.14								
Unidentified sp. 2				1.80	1.88	3.00			
Branchiostegidae	.42								
Caulolatilus sp.	.42								
Sciaenidae				.02					
Mullidae	.21								
Pseudupeneus maculatus	.05								
Unidentified	.16								
Labridae	.16								
Percophididae	.21	1.51	9.1	.79	.97	.62			

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Bembrops maculatus		.80	.10	.08					
B. anatirostris		.71	.05						
B. gobioides			.76	.06	.87	.13			
B. magnisquamis				.65	.10	.49			
Bembrops sp.	.21								
Uranoscopidae	2.29	.17	.05						
Kathetostoma cubana	2.29	.17	.05						
Gempylidae	.26	1.09	.62	1.25	.34	.19	.08		
Gempylus serpens				.91	.34	.16			
Epinnula o. americana	.26	1.09	.60	.22					
Unidentified sp.			.02	.12		.03	.08		
Trichiuridae		.03							
Scorpaenidae	7.55	1.87	1.85	4.14	.10	3.26			
Setarches guentheri			1.13	4.08	.10	3.26			
Unidentified sp.			.72	.06					
Triglidae	7.55	1.87	.34						
Bellator brachychir	4.32	8.38	.21						
B. militaris	3.80	1.78							
B. egretta	.16	.29							
Prionotus stearnsi		6.11							
Prionotus sp.		.20	.13						
Peristediidae	.36	.89	.90	4.36	2.31	2.54	.31		
Callionymidae		.03	.15	.04	.05	.07			
Callionymus agassizi		.03	.15	.04	.05	.07			
Brotulidae	.21	.11	.21	.73	.72	1.08	8.16	.52	2.38

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Ophidiidae	3.18	6.37	.51	.63		.07			
Stromateidae		.09	.02	.06					
Cubiceps nigriargenteus?		.09	.02	.06					
Bothidae	12.14	1.10	.11	.12					
Citharichthys cornutus	7.92	.12							
Gastropsetta frontalis	.10								
Cyclopsetta fimbriata	.21								
Chascanopsetta sp.			.03						
Unidentified	3.91	.98	.08	.12					
Pleuronectidae		2.15	2.64	2.18					
Cynoglossidae	.05								
Symphurus sp.	.05								
Triacanthodidae	.31	1.67	.80	1.31	.05	.46			
Hollardia hollardi	.31	1.61	.30						
Parahollardia schmidti		.06	.38	1.29	.05·	.46			
Johnsonina eriomma			.12	.02					
Tetraodontidae	.16								
Sphoeroides sp.	.16								
Batrachoididae	20.05	2.93							
Porichthys porosissimus	20.05	2.93							
Lophiidae	.26	.11	.05	.10		.06			
Chaunacidae		1.71	6.18	12.00	5.43	5.35	.23		
Chaunax pictus		1.71	6.18	12.00	5.43	5.35	.23		
Ogcocephalidae	6.61	.29	.58	2.18	1.01	3.81	.84		
Halieuthichthys aculeatus	4.84	.17						.10	

APPENDIX I (Cont.)

Depth range (fathoms)	75 100	101 150	151 200	201 250	251 300	301 350	351 400	401 450	451 500
Ogcocephalus parvus	1.61	.03	.07						
Ogcocephalus sp.	.16	.06	.08						
Dibranchus atlanticus		.03	.43	2.18	1.01	3.81	.84	.10	